An SSR genetic map of *Sorghum bicolor* (L.) Moench and its comparison to a published genetic map

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Abstract: *Sorghum bicolor* (L.) Moench is an important grain and forage crop grown worldwide. We developed a simple sequence repeat (SSR) linkage map for sorghum using 352 publicly available SSR primer pairs and a population of 277 F_2 individuals derived from a cross between the Westland A line and PI 550610. A total of 132 SSR loci appeared polymorphic in the mapping population, and 118 SSRs were mapped to 16 linkage groups. These mapped SSR loci were distributed throughout 10 chromosomes of sorghum, and spanned a distance of 997.5 cM. More important, 38 new SSR loci were added to the sorghum genetic map in this study. The mapping result also showed that chromosomes SBI-01, SBI-02, SBI-05, and SBI-06 each had 1 linkage group; the other 6 chromosomes were composed of 2 linkage groups each. Except for 5 closely linked marker flips and 1 locus (Sb6_34), the marker order of this map was collinear to a published sorghum map, and the genetic distances of common marker intervals were similar, with a difference ratio ≤ 0.05 between the 2 maps. The difference ratio is a new index developed in this study that can be used to compare the genetic distances of DNA markers between 2 maps. This SSR map carrying additional SSR markers will facilitate mapping quantitative trait loci to the sorghum genome and map-based gene cloning. Furthermore, the novel method for calculating distance between DNA markers will be a useful tool for the comparative analysis of genetic markers between linkage maps with different genetic backgrounds and the alignment of different sorghum genetic maps.

Key words: comparative mapping, linkage map, map alignment, microsatellite, SSR markers.

Résumé : Le *Sorghum bicolor* (L.) Moench est une culture céréalière et fourragère importante cultivée mondialement. Les auteurs ont développé une carte génétique pour le sorgho à l'aide de 352 paires d'amorces microsatellites (SSR) disponibles publiquement et d'une population de 277 individus F_2 issus d'un croisement entre la lignée Westland A et PI 550610. Cent trente-deux (132) locus SSR semblent polymorphes au sein de la population et 118 ont été assignés à l'un de seize groupes de liaison. Ces locus cartographiés étaient distribués sur les 10 chromosomes du sorgho et s'étendaient sur une distance de 997,5 cM. Fait plus important, 38 des locus SSR ont été placés sur la carte du sorgho pour la première fois. L'analyse de la carte a montré que les chromosomes SBI-01, 02, 05 et 06 étaient constitués d'un seul groupe de liaison tandis que les six autres chromosomes étaient chacun composés de deux groupes de liaison. Sauf pour cinq inversions de marqueurs très rapprochés et du locus Sb6_34, l'ordre des marqueurs sur cette carte est identique à une carte du sorgho publiée précédemment et les distances entre marqueurs communs étaient semblables puisque le ratio des différences entre les deux cartes était inférieur à 0,05. Le ratio des différences est un nouvel indice, développé au cours de ce travail, qui permet de comparer les distances génétiques entre marqueurs chez deux cartes. Cette carte de SSR comprenant des marqueurs SSR additionnels facilitera la cartographie de QTL dans le génome du sorgho ainsi que le clonage positionnel. De plus, la nouvelle méthode pour calculer la distance entre marqueurs sera un outil utile pour la comparaison des marqueurs génétiques chez des cartes génétiques assemblées à partir de lignées dotées de fonds génétiques distincts et pour l'alignement de différentes cartes génétiques du sorgho.

Mots clés : cartographie comparée, carte de liaison, alignement de cartes, microsatellite, marqueurs SSR.

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Introduction

DNA simple sequence repeats (SSRs), also known as microsatellites, are mostly codominant markers, and can be easily amplified with PCR and detected with agarose gel electrophoresis. SSRs are highly polymorphic in sorghum (*Sorghum bicolor* (L.) Moench) (Brown et al. 1996; Taramino et al. 1997; Tao et al. 1998; Kong et al. 2000; Bhattramakki et al. 2000), except those located in coding regions that are relatively conservative (Schloss et al. 2002).

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Although traditional methods for the development of SSR markers are complex (Brown et al. 1996; Bhattramakki et al. 2000), this will become much easier after completion of the sorghum sequencing project (Kresovich et al. 2005). SSR markers have been widely used in studies of genetic diversity among elite inbred lines (Smith et al. 2000; Menz et al. 2004), among germplasm collections from different geographic locations (Yang et al. 1996; Dje et al. 2000), and in the assessment of population genetic structure and relatedness within or among land races (Dje et al. 1999; Ghebru et al. 2002; Uptmoor et al. 2003; Folkertsma et al. 2005). SSRs have been used to construct the framework architecture of a highly dense genetic map (Menz et al. 2002), and to bridge maps developed in different laboratories. One recent example is the alignment of genetic maps constructed with 2 populations that share 1 common parent (BTx623), but have different alternate parents, using shared SSRs as reference points (Feltus et al. 2006).

SSR marker technology has proven to be a dependable, rapid, and inexpensive tool for plant genotyping (Yang et al. 1996). SSR markers are becoming the markers of choice for plant genome analysis because of their highly polymorphic and informative nature. As a result, they have been increasingly used as DNA markers to construct linkage maps in various populations of sorghum. Taramino et al. (1997) mapped 7 SSR loci to 5 linkage groups, using an existing sorghum restriction fragment length polymorphism (RFLP) map. Similarly, Tao et al. (1998, 2000) assigned 8 new SSR markers to an RFLP linkage map. Kong et al. (2000) and Bhattramakki et al. (2000), using the same population, mapped 31 and 113 new SSR markers, respectively, on a previously developed RFLP linkage map. Later, the combination of mapped SSRs as a framework and additional amplified fragment length polymorphism (AFLP) markers permitted the construction of a high-density genetic map (Menz et al. 2002). Feltus et al. (2006) added 15 additional new SSRs, which were used as bridge markers for map alignment among different genetic maps (Bhattramakki et al. 2000; Kong et al. 2000; Menz et al. 2002; Bowers et al. 2003). Sorghum SSR linkage maps containing more markers in different genetic backgrounds by different mapping groups are still needed, and the mapping information from all these maps should be integrated (Bennetzen et al. 2001).

Various linkage maps of sorghum are being rapidly developed. To use those maps more efficiently, there is a need to integrate the molecular information from various maps among genotypes. In addition to comparing the marker orders along chromosomes, there is a need to calculate the differences between intervals with the same flanking markers for each chromosome. Herein, we derive a formula from the distance measurement of interval variables, proposed by Gower (1971), to quantify genetic-distance differences between different molecular maps.

In this paper, we report the construction of a sorghum map of 118 SSR markers using an F_2 population of 227 individuals from a new genetic background. Among the mapped SSRs, 38 are new tothis map. The map has added value in the areas of gene isolation by map-based cloning and comparative genome analysis. Using the above-mentioned method, we compared our map with a previously published sorghum map, based on map positions of common loci, which provided strong support for the alignment of 2 genetic maps.

Materials and methods

Linkage mapping of SSR markers was performed using a population of 277 F_2 individuals, derived from a cross between the Westland A line and PI 550610. The Westland A line was developed from 'Wheatland', which originated from an early milo-type introduction from Kenya (Karper 1944; NGPS 2006). PI 550610 originated in Syria and was introduced, via the Kuban Experimental Station, Krasnodar Province of Russia, to the Unites States (Andrews et al. 1993). This population was also used for molecular mapping of the quantitative trait loci (QTLs) for greenbug resistance (Wu and Huang 2006).

Plant genomic DNA was extracted from leaf tissue for each of the 277 F_2 plants and parents, in accordance with the cetyltrimethylammonium bromide (CTAB) procedure described by Doyle and Doyle (1990). DNA solutions, adjusted to a concentration of 10 ng/μL, were used as the templates for PCRs.

A collection of 352 SSR primer pairs were amassed for this study from the publications of Brown et al. (1996), Taramino et al. (1997), Dean et al. (1999), Bhattramakki et al. (2000), Kong et al. (2000), Cordeiro et al. (2001), and Schloss et al. (2002). The primers were synthesized by Invitrogen Corporation (Carlsbad, Calif.). The 352 SSR primer pairs were preliminarily screened for polymorphisms, using the template DNA samples obtained from the 2 parents and 2 randomly selected F_2 plants. SSR PCRs were conducted in 96-well PCR plates in a PTC-220 Dyad Thermal Cycler (MJ Research Inc., Waltham, Mass.). The thermal cycles for the SSR PCRs were programmed for an initial denaturation of 5 min at 94 °C; followed by 14 cycles of 20 s at 94 °C, 1 min at 58 °C, and 30 s at 72 °C; 28 cycles of 20 s at 94 °C, 1 min at 55 °C, and 30 s at 72 °C; and a final 10 min extension at 72 °C. The SSR PCR mixtures (10.85 μL in total) consisted of 4.47 μL H_2O, 0.67 μL of 10× reaction buffer, 0.40 μL 25 mmol $MgCl_2$/L, 0.13 μL 10 mmol deoxynucleoside triphosphate (dNTP)/L, 1.34 μL of 1 mmol SSR forward primer/L tailed with M13 forward primer sequence (5′-CACGACGTTGTAAAACGACG-3′), 1.34 μL of 1 mmol SSR reverse primer/L, 1 μL of 1 mmol M13 forward primer/L labeled with florescence dye either at 700 nm or 800 nm (LI-COR Inc., Lincoln, Nebr.), and 1.5 μL of 10 ng/μL template DNA. PCR products from a plate labeled with 700 nm fluorescent dye and from another plate labeled with 800 nm dye (LI-COR Inc.) were pooled and mixed thoroughly, loaded into wells of 6.5% KB^{Plus} gel (LI-COR Inc.), and run in a 4300 DNA Analyzer (LI-COR Inc.). For codominant SSR markers, gel images were visually scored for each DNA sample from the F_2 population and for parental plants, and recorded as A for a homozygote for the allele from the Westland A line, as B for a homozygote for the allele from PI 550610, as H for a heterozygote carrying both alleles, and as "–" for a missing lane. For a few dominant SSR markers, a resultant band was scored as D, and a missing band as "–". All genotyping data were read

into the Microsoft Excel data matrix, and then exported into a "raw" text data file for genetic analysis.

A genetic linkage map was constructed using MapMaker/EXP 3.0 (Lander et al. 1987), with a threshold value of the logarithm of odd ratio (LOD) ≥ 5.0, and maximum genetic distance of 37.5 cM. Anchor markers were selected on the basis of "group" results; these markers, previously mapped with known chromosome identity and grouped with other nonmapped markers, served as anchor markers. For each chromosome, 2 to 5 anchor markers were selected, depending on how many covered a distance of 10 to 30 cM between neighboring anchor markers; each marker had to have at least 270 unambiguously scored data points. The Kosambi mapping function was used to convert the recombination fractions to genetic distance (cM) (Kosambi 1944). The linkage groups of SSR markers were assigned to sorghum chromosomes, in accordance with the methods described by Bhattramakki et al. (2000) and Menz et al. (2002); in the final map, we adopted the nomenclature of the chromosome designation system developed by Kim et al. (2005). Multipoint analysis commands (make chromosome, anchor, assign, order, and framework) were used in the linkage analysis, as described in the MapMaker/EXP 3.0 user manual (Lincoln et al. 1992).

The distance measurement of interval variables between 2 individuals, proposed originally by Gower (1971), was used to develop a new formula to compare this map with that of Bhattramakki et al. (2000). In Gower's formula, similarity coefficient was defined as $S_{ijk} = 1 - |X_i - X_j|/R_k$, where X_1, X_2, …, X_n were quantitative values of character k for the total sample of n individuals, and R_k was the range value of interval K. In this study, because we had only 2 individuals (i.e., 2 maps of many shared intervals to be compared), and our purpose was to define the length difference of shared intervals for each chromosome, the formula was modified as

$$\text{difference ratio} = \frac{\sum |A_{ik} - B_{ik}|}{A_i + B_i}$$

where A_{ik} is the length (cM) of kth shared marker interval on ith chromosome of map A, and B_{ik} is the length (cM) of kth shared marker interval on ith chromosome of map B. The $\sum |A_{ik} - B_{ik}|$ is an additively absolute value of the length difference of each shared marker interval on ith chromosome between maps A and B, and $(A_i + B_i)$ represents an additive value of all shared intervals for ith chromosome of maps A and B, which is used to normalize the difference value, $\sum |A_{ik} - B_{ik}|$.

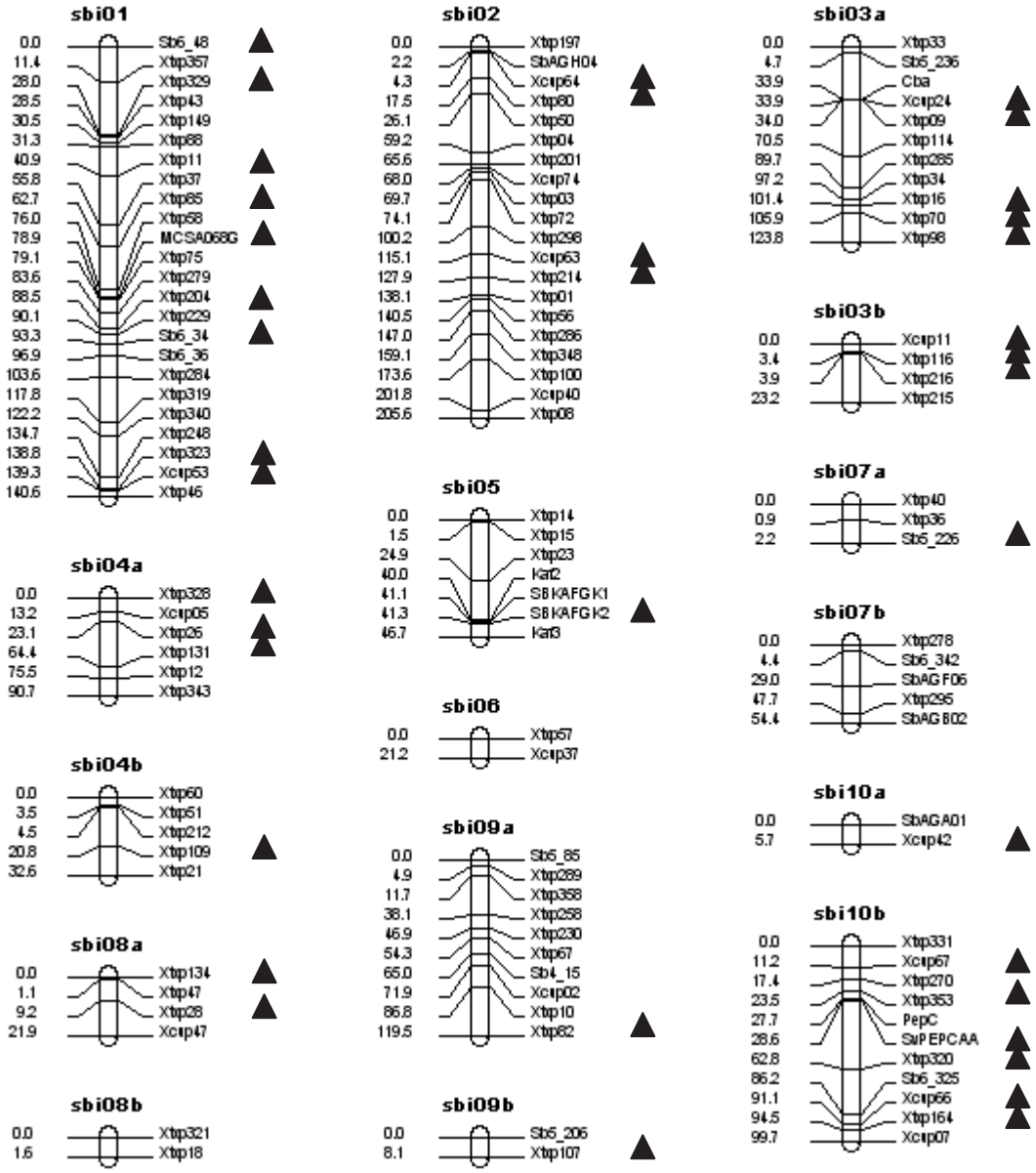
Results and discussion

In this study, the 352 previously reported SSR markers were screened in a sorghum mapping population of 277 F_2 individuals derived from the cross between the Westland A line and PI 550610, and 132 of those SSR loci were polymorphic among the individuals. Segregation analysis data showed that 107 markers followed the Mendelian ratio of segregation in the progeny, with χ^2 values < 5.99 for codominant markers and < 3.84 for dominant markers ($P > 0.05$); 25 codominant markers (18.9%) had χ^2 values ranging from 6.0 to 377.5. Among the 25 markers deviating from normal segregation, 8 (Xtxp79, Xtxp91, Xtxp213, Xtxp224, Xtxp267, Xtxp290, Xcup01, and Xcup06) were excluded from linkage analysis to prevent erroneous results, because they were not mapped previously and had χ^2 values > 11 ($P < 0.005$). Three previously mapped markers (Xtxp210, Xtxp302, and SbAGB03) were also excluded from the linkage analysis because they had χ^2 values from 17.25 to 377.5, and mapping locations were different from previous reports (Bhattramakki et al. 2000; Taramino et al. 1997). There are numerous reasons for the distorted segregation ratios repeatedly observed in sorghum mapping experiments (Chittenden et al. 1994; Xu et al. 1994; Dufour et al. 1997; Tao et al. 1998). Tao et al. (1998) suggested that one of the main reasons for distorted segregation is the elimination of gametes or zygotes by a lethal factor located in a neighboring region of the marker. The aberrant loci observed in this mapping population were probably associated with some lethal loci. Xtxp210, Xtxp302, and SbAGB03 were mapped to SBI-08, SBI-01 (Bhattramakki et al. 2000), and SBI-02 (Taramino et al. 1997). Menz et al. (2002) also reported a distorted region on SBI-01, where Xtxp302 resided, and another region on SBI-08, where Xtxp210 was located.

A new sorghum genetic map was constructed (Fig. 1), which comprised 118 segregating SSR loci, including 38 novel map locations. The map covered 997.5 cM, with an average distance of 8.5 cM between markers. According to linkage analysis, 16 linkage groups were identified (published SSR markers were used as anchors) (Bhattramakki et al. 2000) and subsequently named on the basis of the chromosome identity system (Kim et al. 2005). Four chromosomes (SBI-01, SBI-02, SBI-05, and SBI-06) had 1 linkage group each, whereas 6 other chromosomes were mapped to 2 linkage groups each. The linkage group length for each chromosome varied from 21.2 cM on SBI-06 to 205.6 cM on SBI-02 (Fig. 1). The number of SSR markers per chromosome varied from 2 on SBI-06 to 24 on SBI-01. Twenty-four SSRs were mapped to SBI-01, including 9 new loci, which covered a distance of 140.6 cM. The linkage group corresponding to SBI-02 was the longest, and spanned a distance of 205.6 cM. This group contained 20 markers, of which 4 were newly placed on the map. Linkage groups SBI-03a and SBI-03b together covered a distance of 147 cM and included 15 SSRs, with 8 loci newly assigned to this chromosome. Similarly, SBI-04a and SBI-04b, SBI-07a and SBI-07b, SBI-08a and SBI-08b, SBI-09a and SBI-09b, and SBI-10a and SBI-10b covered respective distances of 123.3, 56.6, 23.5, 127.6, and 105.4 cM, and were mapped with 11(4 new), 8 (1 new), 6 (2 new), 12 (2 new), and 13 (7 new) markers, respectively. SBI-05 and SBI-06 covered relatively short genetic distances, with 7 (1 new) and 2 (0 new) SSR markers being mapped, respectively. In addition to the 80 SSR markers mapped on previous maps, we report 38 new SSR loci added to the sorghum genetic map.

To compare the order of consecutive markers in this map, the map developed by Bhattramakki et al. (2000) was used (their map contained 147 SSRs, which is the largest number of SSRs mapped for sorghum to date). There are 64 SSRs common between the 2 SSR linkage maps. Good colinearity of the marker order was observed along most of the chromosomes or linkage groups, except 1 marker (Sb6-34) and 5 pairs of consecutive markers. Sb6-34 was mapped in the middle region on SBI-01 in this study, but in a distal region

Fig. 1. A linkage map of *Sorghum bicolor*, based on 118 simple sequence repeat (SSR) markers. Linkage groups were named according to the nomenclature of sorghum chromosomes (Kim et al. 2005). In cases where 2 groups were mapped for a chromosome, the 'a' and 'b' appearing after a chromosome number represent the chromosomal region close to the short and long arms, respectively. Numbers shown to the left of linkage groups indicate cumulative map distances, in cM (Kosambi estimates). All SSR locus names are shown on the right side of the linkage groups. Markers with names followed by ▲ are the newly added SSR loci.



of SBI-08 in the study by Bhattramakki et al. (2000). The 5 pairs of consecutive markers showed order rearrangements: Xtxp229 and Sb6-36 on SBI-01, Xtxp03 and Xtxp72 on SBI-02, Xtxp51 and Xtxp212 on SBI-04, Xtxp14 and Xtxp15 on SBI-05, and Xtxp331 and Xtxp270 on SBI-10. Flips are a common feature of closely spaced markers. Feltus et al. (2006) observed the same phenomenon when conducting an alignment study of an interspecific map with an intraspecific map. The rearrangements could be real or simply the result of errors in genotyping in either of the populations. Such errors can occur, especially when mapping population sizes are small (Feltus et al. 2006).

For the convenience of comparing the genetic distances for each chromosome in the 2 maps, we developed an index, which we call the difference ratio, that was derived from the equation for the distance measurement (Gower 1971). Both the equations for the distance measurement and the difference ratio are similar in the numerator, but different in the denominator. In a comparison of the genetic distances of this map with the published sorghum map (Bhattramakki et al. 2000), the difference ratio was calculated for each chromosome (Table 1). Overall, 50 marker intervals were shared by the 2 maps. The difference ratio in genetic distance between the 2 maps was 0.05; the value of each chromosome ranged from 0.04 (SBI-02 and SBI-05) to 0.74 (SBI-10). The difference ratios of SBI-08 and SBI-10 were high because the size of sampling intervals was small, 1 and 2 for each, respectively.

Table 1. The difference ratio of genetic distance in the common marker intervals between map A, developed in this study, and map B, developed by Bhattramakki et al. (2000).

Chromosome ID	No. of shared marker intervals	A_i (cM)	B_i (cM)	$\sum \lvert A_{ik} - B_{ik} \rvert$ (cM)	$(A_i + B_i)$ (cM)	Difference ratio
SBI-01	14	129.2	147.2	18	276.4	0.07
SBI-02	12	205.6	189.8	15.8	395.4	0.04
SBI-03	5	97.2	76.9	20.3	174.2	0.12
SBI-04	4	47.8	35.3	12.5	83.2	0.15
SBI-05	4	46.7	43.7	3.0	90.4	0.04
SBI-06	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
SBI-07	3	48.6	56.0	7.4	104.6	0.07
SBI-08	1	1.6	6.0	4.4	7.6	0.58
SBI-09	5	81.9	67.3	14.6	149.2	0.10
SBI-10	2	27.7	4.1	23.6	31.8	0.74
Total	50	686.3	626.3	60.0	1312.6	0.05

Note: n.a., not applicable.

In summary, an SSR map of sorghum was constructed with 118 markers, covering a distance of approximately 1000 cM. Among the mapped SSR loci, 38 had not been previously placed on the sorghum genetic map. When compared with the map of Bhattramakki et al. (2000), there are 64 SSR markers in common, 50 shared marker intervals between the 2 maps, a high collinearity in the marker order, and a low difference ratio in genetic distance. This SSR map is an additional resource for the genetic study of sorghum, including QTL-mapping and map-based cloning of important genes. The addition of novel SSR markers to the sorghum map will make it useful for molecular mapping in other sorghum populations.

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References

Andrews, D.J., Bramel-Cox, P.J., and Wilde, G.E. 1993. New sources of resistance to greenbug, biotype I, in sorghum. Crop Sci. **33**: 198–199.

Bennetzen, J.L., Subramanian, V., Xu, J., Salimath, S.S., Bhattramakki, D., and Hart, G.E. 2001. A framework genetic map of sorghum containing RFLP, SSR and morphological markers. *In* DNA-based markers in plants. *Edited by* R.L. Phillips and I.K. Vasil. Kluwer Academic Publishers, Netherlands. pp. 347–355.

Bhattramakki, D., Dong, J., Chhabra, A.K., and Hart, G.E. 2000. An integrated SSR and RFLP linkage map of *Sorghum bicolor* (L.) Moench. Genome, **43**: 988–1002. doi:10.1139/gen-43-6-988. PMID:11195353.

Bowers, J.E., Abbey, C., Anderson, S., Chang, C., Draye, X., Hoppe, A.H., et al. 2003. A high-density genetic recombination map of sequence-tagged sites for Sorghum, as a framework for comparative structural and evolutionary genomics of tropical grains and grasses. Genetics, **165**: 367–386. PMID:14504243.

Brown, S.M., Hopkins, M.S., Mitchell, S.E., Senior, M.L., Wang, T.Y., Duncan, R.R., et al. 1996. Multiple methods for the identification of polymorphic simple sequence repeats (SSRs) in sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet. **93**: 190–198. doi:10.1007/s001220050265.

Chittenden, L.M., Schertz, K.F., Lin, Y.R., Wing, R.A., and Paterson, A.H. 1994. A detailed RFLP map of *Sorghum bicolor* × *S. propinquum*, suitable for high density mapping, suggests ancestral duplication of Sorghum chromosomes or chromosomal segments. Theor. Appl. Genet. **87**: 925–933.

Cordeiro, G.M., Casu, R., McIntyre, C.L., Manners, J.M., and Henry, R.J. 2001. Microsatellite markers from sugarcane (*Saccharum* spp.) ESTs cross transferable to erianthus and sorghum. Plant Sci. **160**: 1115–1123. doi:10.1016/S0168-9452(01)00365-X. PMID:11337068.

Dean, R.E., Dahlberg, J.A., Hopkins, M.S., Mitchell, S.E., and Kresovich, S. 1999. Genetic redundancy and diversity among 'Orange' accessions in the U.S. National Sorghum Collection as assessed with simple sequence repeat (SSR) markers. Crop Sci. **39**: 1215–1221.

Dje, Y., Forcioli, D., Ater, M., Lefebvre, C., and Vekemans, X. 1999. Assessing population genetic structure of sorghum landraces from north-western Morocco using allozymes and microsatellite markers. Theor. Appl. Genet. **99**: 157–163.

Dje, Y., Heuertz, M., Lefebvre, C., and Vekemans, X. 2000. Assessment of genetic diversity within and among germplasm accessions in cultivated sorghum using microsatellites markers. Theor. Appl. Genet. **100**: 918–925.

Doyle, J.J., and Doyle, J.L. 1990. Isolation of plant DNA from fresh tissues. Focus, **12**: 13–15.

Dufour, P., Deu, M., Grivet, L., Dhont, A., Paulet, F., Bouet, A., et al. 1997. Construction of a composite sorghum genome map and comparison with sugarcane, a related complex polyploid. Theor. Appl. Genet. **94**: 409–418. doi:10.1007/s001220050430.

Ghebru, B., Schmidt, R.J., and Bennetzen, J.L. 2002. Genetic diversity of Eritrean sorghum landraces assessed with simple sequence repeat (SSR) markers. Theor. Appl. Genet. **105**: 229–236. PMID:12582524.

Gower, J.C. 1971. A general coefficient of similarity and some of its properties. Biometrics, **27**: 857–874. doi:10.2307/2528823.

Feltus, F.A., Hart, G.E., Schertz, K.F., Casa, A.M., Kresovich, S., Abraham, S., et al. 2006. Alignment of genetic maps and QTLs between inter- and intra-specific sorghum populations. Theor. Appl. Genet. **112**: 1295–1305. doi:10.1007/s00122-006-0232-3. PMID:16491426.

Folkertsma, R.T., Frederick, H., Rattunde, W., Chandra, S., Raju, G.S., and Hash, C.T. 2005. The pattern of genetic diversity of

Guinea-race *Sorghum bicolor* (L.) Moench landraces as revealed with SSR markers. Theor. Appl. Genet. **111**: 399–409. doi:10.1007/s00122-005-1949-0. PMID:15965652.

Karper, R.E. 1944. Registration of sorghum varieties, IV. Agron. J. **36**: 453.

Kim, J.S., Klein, P.E., Klein, R.R., Price, H.J., Mullet, J.E., and Stelly, D.M. 2005. Chromosome identification and nomenclature of *Sorghum bicolor*. Genetics, **169**: 1169–1173.

Kong, L., Dong, J., and Hart, G.E. 2000. Characteristics, linkage-map positions, and allelic differentiation of *Sorghum bicolor* (L.) Moench DNA simple sequence repeats (SSRs). Theor. Appl. Genet. **101**: 438–448. doi:10.1007/s001220051501.

Kosambi, D.D. 1944. The estimation of map distances from recombination values. Ann. Eugen. **12**: 172–175.

Kresovich, S., Barbazuk, B., Bedell, J.A., Borrell, A., Buell, C.R., Burke, J., et al. 2005. Toward sequencing the sorghum genome. A U.S. National Science Foundation-sponsored workshop report. Plant Physiol. **138**: 1898–1902. PMID:16172096.

Lander, E.S., Green, P., Abrahamson, J., Barlow, A., Daly, M.J., Lincoln, S.E., and Newburg, L. 1987. MAPMAKER: an interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics, **1**: 174–181. doi:10.1016/0888-7543(87)90010-3. PMID:3692487.

Lincoln, S., Daly, M., and Lander, E. 1992. Constructing genetic maps with MAPMAKER/EXP 3.0. Whitehead Institute Technical Report. 3rd ed. Whitehead Institute for Biomedical Research, Cambridge, Mass.

Menz, M.A., Klein, R.R., Mullet, J.E., Obert, J.A., Unruth, N.C., and Klein, P.E. 2002. A high-density genetic map of *Sorghum bicolor* (L.) Moench based on 2926 AFLP, RFLP and SSR markers. Plant Mol. Biol. **48**: 483–499. doi:10.1023/A:1014831302392. PMID:11999830.

Menz, M.A., Klein, R.R., Unruth, N.C., Rooney, W.L., Klein, P.E., and Mullet, J.E. 2004. Genetic diversity of public inbreds of sorghum determined by mapped AFLP and SSR markers. Crop Sci. **44**: 1236–1244.

NPGS. 2006. Germplasm resources information database. Available from http://www.ars-grin.gov/cgi-bin/npgs/html/acchtml.pl?1137189 [Accessed on 16 March 2006]

Schloss, S.J., Mitchell, S.E., White, G.M., Kukatla, R., Bowers, J.E., Paterson, A.H., and Kresovich, S. 2002. Characterization of RFLP probe sequences for gene discovery and SSR development in *Sorghum bicolor* (L.). Moench. Theor. Appl. Genet. **105**: 912–920. PMID:12582917.

Smith, J.S.C., Kresovich, S., Hopkins, M.S., Mitchell, S.E., Dean, R.E., Woodman, W.L., Lee, M., and Porter, K. 2000. Genetic diversity among elite sorghum inbred lines assessed with simple sequence repeats. Crop Sci. **40**: 226–232.

Tao, Y.Z., Jordan, D.R., Henzell, R.G., and McIntyre, C.L. 1998. Construction of a genetic map in a sorghum recombinant inbred line using probes from different sources and its comparison with other sorghum maps. Aust. J. Agric. Res. **49**: 729–736. doi:10.1071/A97112.

Tao, Y.Z., Henzell, R.G., Jordan, D.R., Butler, D.G., Kelly, A.M., and McIntyre, C.L. 2000. Identification of genomic regions associated with stay green in sorghum by testing RILs in multiple environments. Theor. Appl. Genet. **100**: 1225–1232. doi:10.1007/s001220051428.

Taramino, G., Tarchini, R., Ferrario, S., Lee, M., and Pe, M.E. 1997. Characterization and mapping of simple sequence repeats (SSRs) in *Sorghum bicolor*. Theor. Appl. Genet. **95**: 66–72. doi:10.1007/s001220050533.

Uptmoor, R., Wenzel, W., Friedt, W., Donaldson, G., Ayisi, K., and Ordon, F. 2003. Comparative analysis on the genetic relatedness of sorghum bicolor accessions from Southern Africa by RAPDs, AFLPs and SSRs. Theor. Appl. Genet. **106**: 1316–1325. PMID:12748784.

Wu, Y.Q., and Huang, Y. 2006. Molecular mapping of QTLs for resistance to the greenbug [*Schizaphis graminum* (Rondani)] in *Sorghum bicolor* (Moench). Theor. Appl. Genet. Submitted.

Xu, G.W., Magill, C.W., Schertz, K.F., and Hart, G.E. 1994. An RFLP linkage map of Sorghum bicolor (L.). Moench. Theor. Appl. Genet. **89**: 139–145.

Yang, W., de Oliveira, A.C., Godwin, I., Schertz, K., and Bennetzen, J.L. 1996. Comparison of DNA marker technologies in characterizing plant genome diversity: variability in Chinese sorghums. Crop Sci. **36**: 1669–1676.